Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species

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Abstract

Past research has provided compelling evidence that variation in flooding duration is the predominant factor underlying plant species distribution along elevation gradients in river floodplains. The role of seasonal variation in flooding, however, is far from clear. We addressed this seasonal effect for 10 grassland species by testing the hypothesis that all species can survive longer when flooded in winter than when flooded in summer. We carried out an inundation experiment under simulated conditions of summer and winter flooding in the greenhouse. The results showed that all species survived longer under winter floods than under summer floods. However, responses upon flooding were species-specific. All summer flood-tolerant species had high tolerance for winter floods as well, but summer flood sensitive species survived either a little longer, or dramatically longer when flooded under simulated winter conditions. Next, we examined whether winter or summer survival best predicted the lower distribution limits of the species as measured in a natural flooding gradient after an extremely long winter flood. We found a strong significant relationship between the lower distribution limits of species in the field and their tolerance to summer floods, although we measured the lower limits 14 years after the latest major summer flood. In contrast, no such significant relationship existed with species tolerance to winter floods. Some relatively intolerant species occurred at much higher floodplain elevations as was expected from their tolerance to winter inundation in the experiments. This suggests that zonation patterns as created by occasional summer floods may be maintained for a long time, probably due to the limited ability of species to re-colonise lower positions in the floodplain.

Introduction

Flooding is the predominant environmental factor determining plant distribution in river floodplains. It indirectly determines soil composition through erosion and sedimentation (Day et al., 1988; Henry et al., 1996) and directly affects plant growth by reducing oxygen and light availability (Setter et al., 1997). Tolerance to the direct effects of flooding strongly differs among species and these differences are reflected by species zonation along elevation gradients in river floodplains (Lenssen & de Kroon, 2005). Here, the most tolerant species dominate the lower, frequently flooded positions, whereas intolerant species are restricted to the highest elevations of the floodplain (Squires & Van der Valk, 1992; Carter & Grace, 1990; Sand-Jensen & Frost-Christensen, 1999; He et al., 1999; Vervuren et al., 2003; Van Eck et al., 2004). This tight correlation between flooding tolerance and elevational position indicates that tolerance may be an important tool to predict species responses to changes in river flooding regimes as a consequence of global warming, canalization or floodplain excavation.

However, before accurate predictions can be made it may be necessary to gain further
understanding of how various components of the flooding regime affect a species tolerance and how this in turn determines a species elevational distribution in floodplains. For instance, it has clearly been shown that sediment load of the flood water decreases plant survival by reducing light availability of submerged plants (Vervuren et al., 2003; Mommer et al., 2005). Season may be an equally important component of flooding regime, particularly in temperate zones where seasonal variation has a profound impact on water temperature and annual plant growth cycles.

Field observations and experiments indicate dramatic impacts of floods during the growing season (hereafter referred to as summer) on species’ lower distribution limits, i.e. species’ lowest position along the flooding gradient (Sykora et al., 1988; Vervuren et al., 2003; Van Eck et al., 2004). Winter floods have always been assumed to exert little direct effects, either because plants may be metabolically inactive during winter ( Klimesová, 1994; Siebel, 1998), the low water temperature reduces respiration (Van Eck et al., 2005a) or because of relatively high oxygen concentration in cold water (Pedersen et al., 1998). Accordingly, the few available experiments have demonstrated a mild impact of winter floods, although these studies were limited to three species at most (Klimesová, 1994; Siebel, 1998; Van Eck et al., 2005a). A broader interspecific comparison of summer and winter floods has thus far been lacking. Such experiments, however, are required to evaluate the importance of the seasonal component of flooding regime, because observations have indicated that some summer flood-intolerant species are also sensitive to winter floods (Studer-Ehrensberger et al., 1993; Crawford et al., 2003; Crawford, 2003). Moreover, winter floods may be more important for field distribution because, at least in most rivers of the temperate zone, these will be more frequent and of longer duration due to excess rainfall and melting snow during winter and early spring (Day et al., 1988; Breen et al., 1988; Nilsson et al., 1991; Vervuren et al., 2003).

To gain further understanding of the role of the seasonal component of a river’s flooding regime we extended the comparison of summer and winter flooding to 10 grassland species. We first tested the hypothesis that all species are less tolerant to summer flooding and that flooding during winter will enhance tolerance for all species with a similar magnitude, i.e. that the effect of season on tolerance is not species specific. Next, we tested the hypothesis that field distribution of floodplain species after a relatively extreme winter flooding would reflect their tolerance to winter floods. We tested these hypotheses because we assumed that the seasonal component of flooding regime would only be important if it changes the hierarchy of species tolerances. Only then may winter floods be expected to produce a different zonation pattern than summer floods. As a measure of flood tolerance we estimated LT50, the flooding duration (Lethal Time) after which 50% of the plants had died (Vervuren et al., 2003). Earlier work has shown that LT50 is the measure of flood tolerance that best predicts elevational distribution in floodplains (Van Eck et al., 2004).

Materials and methods

Plant material and pre-treatments

The impact of simulated summer and winter floods on species survival was investigated for 10 grassland species that inhabit different floodplain elevation ranges along the lower Rhine. The following species were selected: *Alopecurus pratensis* L., *Arrhenatherum elatius* (L.) J. and C. Presl, *Daucus carota* L., *Elytrigia repens* (L.) Nevski, *Festuca rubra* L., *Medicago falcata* L., *Plantago lanceolata* L., *Rumex acetosa* L., *Rumex crispus* L. and *Rumex thyrsiflorus* Fingerh. All species are relatively long-lived (hemi cryptophytes with winter buds just below the soil surface) and therefore likely to encounter flooding during the winter as adults. Seeds were collected in 1996 and 1998 from single populations in floodplain grasslands along the river Waal, the main and free flowing branch of the river Rhine in the Netherlands, and stored at room temperature under dry and dark conditions.

Seeds were germinated on moist filter paper in petri dishes and placed in a growth cabinet (12 h 25 μmol m⁻² s⁻¹ PPFR (Philips TL33), 25 ºC; 12 h dark, 10 ºC). In October 1999, germinated seeds were individually transferred into